

HABITAT CHARACTERISTICS IN THE CORE BREEDING RANGE OF THE SWAINSON'S WARBLER

GARY R. GRAVES^{1,2}

ABSTRACT.—I investigated the physiognomic and floristic characteristics of Swainson's Warbler (*Limnothlypis swainsonii*) territories at five localities within its core breeding range in Arkansas, Mississippi, Louisiana, and Florida. The warbler attained its greatest abundance (10–20 territorial males/km²) in floodplain forest characterized by small (<25 cm dbh) trees (ca 620–820 stems/ha) and understory thickets of saplings, vines, and shrubs (ca 35,000–48,000 small woody stems/ha). Territories in mature forest typically were associated with disturbance gaps. Canopy height, basal area, and floristics appear to be relatively unimportant factors in habitat selection, provided that understory requirements are met, which explains the warbler's occurrence in regenerating clearcuts as well as in relic tracts of old growth forest. Giant cane (*Arundinaria gigantea*), hypothesized to be an essential habitat requisite along the northern periphery of its breeding range, was sparse or absent in the prime breeding locations surveyed in this study. Selective thinning and clearcutting are viable habitat management techniques for the Swainson's Warbler. Received 28 August 2001, accepted 28 February 2002.

The success of management programs for Nearctic-Neotropical migratory birds ultimately will depend upon a thorough understanding of the fundamental habitat requirements of breeding and wintering populations. This understanding typically is acquired in incremental phases, beginning with the compilation of life history anecdotes and narrative descriptions of habitat (Brewster 1885, Wayne 1886, Widmann 1895) and the mapping of breeding and wintering distributions (Robbins et al. 1992, Remsen 2001). Once general habitat preferences are known, research customarily shifts toward the quantification of habitat structure (Eddleman et al. 1980), investigation of nesting and foraging microhabitats (Robinson and Holmes 1984, Parrish 1995, Graves 1998), surveys of geographic variation in habitat structure (Dow 1968; Collins 1983a, 1983b; James et al. 1984), and the correlation between measurable features of the environment and distribution and abundance of populations (Orians and Wittenberger 1991, Stowe et al. 1993). In the final phase, researchers examine the influence of spatial and compositional attributes of habitat on the fecundity and viability of populations (James et al. 1997). Although considerable progress in habitat analysis has been made during the past 50 years (Wiens 1989), investigative studies

on the majority of migratory species are still firmly mired in the secondary phase of diagnosis and quantification (see accounts in Poole et al. 1992–1993; Poole and Gill 1993–1997; 1998–2002).

This paper addresses the physiognomic and floristic characteristics of habitat in the core breeding range of the Swainson's Warbler (*Limnothlypis swainsonii*). Though locally common in the lower Mississippi Valley and on the coastal plain from eastern Texas to southeastern Virginia (Meanley 1971, Brown and Dickson 1994, Graves 1998, Winker et al. 2000), this warbler currently is ranked as the second most endangered breeding songbird in the southeastern United States because of habitat destruction on its breeding range, relatively low population density, and a small wintering range in the Caribbean basin (Morse 1989; Terborgh 1989; Hunter et al. 1993, 1994; Smith et al. 1993; Thompson et al. 1993; Brown and Dickson 1994; Rappole 1995; Mueller et al. 2000). Despite the attention and financial resources focused on the Swainson's Warbler by conservation organizations over the past two decades, surprisingly little is known about its fundamental breeding habitat requirements (Graves 2001). Narrative descriptions of habitat are plentiful, but these offer only a fragmentary characterization of the factors relevant to the warbler's breeding biology (e.g., Brewster 1885; Wayne 1886; Beckham 1887; Widmann 1895; Brooks and Legg 1942; Meanley 1945, 1966, 1969, 1971; Sims and DeGarmo 1948; Brown and Dickson

¹ Dept. of Systematic Biology, MRC-116, P.O. Box 37012, National Museum of Natural History, Smithsonian Inst., Washington, D.C. 20013-7012, USA.

² Corresponding author;
E-mail: graves.gary@nmnh.si.edu

1994; Graves, 1992, 1998; Carrie 1996; Graves et al. 1996). As a direct consequence of the warbler's secretive behavior and large territory size (3–18 ha), and the difficulty of conducting field work in the inhospitable, frequently impenetrable, floodplain habitat favored by this species, the critical mass of quantitative data required for the design and implementation of sound conservation policy is lacking.

Quantitative studies of the physiognomy and floristics of Swainson's Warbler habitat have been conducted in its core breeding range in South Carolina (Peters 1999) and Louisiana (Bassett 2001), and near the northern margin of the breeding range in Illinois (Eddleman 1978, Eddleman et al. 1980), Missouri (Thomas et al. 1996), and the Great Dismal Swamp, Virginia (Graves 2001). Conclusions drawn from these studies, however, are somewhat contradictory. Most notably, Eddleman et al. (1980) and Thomas et al. (1996) stressed the importance of giant cane (*Arundinaria gigantea*) as a critical component in habitat restoration plans for declining populations of Swainson's Warblers in Illinois and Missouri. However, substantial populations of Swainson's Warblers are known to occur in many localities within the core breeding range where cane is either scarce or absent (Graves 2001). Such geographic variation in habitat use is a well-known behavioral phenomenon among passerine birds and correlations between habitat occupancy and specific components of breeding habitat frequently exhibit significant regional fluctuations (Dow 1968; Collins 1983a, 1983b; James et al. 1984). Collectively, these studies suggest that habitat management and conservation efforts in the core breeding range of the Swainson's Warbler should not be predicated on data obtained from geographically peripheral populations.

This study was not designed to evaluate habitat selection of the Swainson's Warbler—the comparison of occupied sites to those available within a local area. Rather, my objective was to evaluate geographic variation in the physiognomic and floristic characteristics of territories in order to address three principal questions: (1) Does the physiognomy of territories vary geographically? (2) Is giant cane an essential element of breeding habitat? (3) Are there regional differences in the litter-pro-

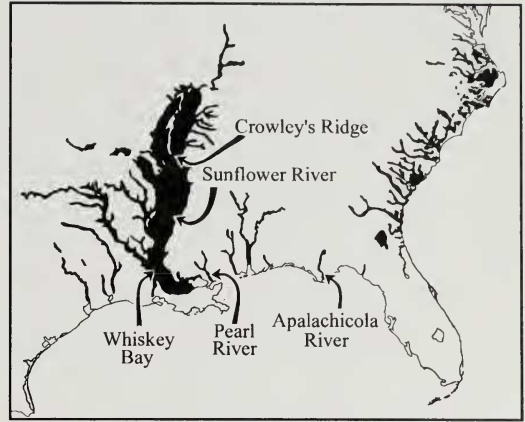


FIG. 1. Study sites depicted in the potential distribution (black) of floodplain deciduous forest and pocosins in the southeastern United States (redrawn from Kuchler 1966), which support the bulk of contemporary breeding populations of Swainson's Warbler.

ducing tree species found on territories? Finally, I discuss the pertinence of physiognomic and floristic data to habitat management programs.

METHODS

Habitat assessment.—I censused breeding populations of Swainson's Warblers along transects in large (>8,000 ha) tracts of floodplain forest on public lands (Fig. 1) with the aid of "playback-and-follow" trials (Graves 1996). The location of territories was recorded on soil survey maps prepared by the USDA Soil Conservation Service. I randomly chose territories for habitat analysis. Employing the sampling methods outlined by Graves (2001), I centered a circular sampling plot (0.045 ha, diameter = 24 m) at the first terrestrial site in each territory at which the undisturbed male was observed to both sing and forage ($n = 49$ territories). The Swainson's Warbler is a terrestrial dead leaf specialist that feeds primarily on litter arthropods whose availability is linked to the characteristics of soil and leaf litter (Graves 1998, 2001). A substantial body of data indicates that males and females use similar foraging microhabitats (Graves 1998). Sampling at dual purpose singing-foraging sites ensured that the physiognomic and floristic data obtained actually corresponded to microhabitats used by Swainson's Warblers. I located sampling plots 40–200 m from roadsides to minimize edge effects, although Swainson's Warblers may actually prefer roadside habitat in certain instances (Graves 2001). Four additional plots in the Whiskey Bay study area (see site descriptions, below) were centered at active nests near singing stations. Data from these nesting sites were collected after the nests were destroyed by predators or the young had fledged.

I measured 14 habitat characteristics in each plot (one plot per territory). Trees (>5 cm dbh) occurring in 0.045-ha plots were measured to the nearest cm and identified to species. I calculated basal area from raw field measurements, whereas stem diameter was converted to size class for comparison. I identified and counted all woody vines supported by trees (at 1.4 m above ground). I also identified and counted small woody stems (<5 cm dbh; i.e., shrubs, tree saplings, woody vines, cane) in four circular subplots (12.6 m², diameter = 4 m) positioned at the cardinal compass coordinates on the perimeter of the 0.045-ha plot. I obtained exact counts by clipping all small stems within each circular subplot at a height of 0.5 m above ground.

Flooding has a profound influence on habitat occupancy patterns of the Swainson's Warbler (Meanley 1966, 1971; Graves 2001). I did not incorporate hydrological data (presence of standing or pooled water) in the analyses, however, because of variation in the interval (1–78 days) between the marking of foraging sites and the subsequent collection of vegetation data.

Site descriptions.—I conducted the study at five sites (Fig. 1). (1) Crowley's Ridge (34° 38' N, 90° 39' W), St. Francis National Forest, Lee and Phillips counties, Arkansas. This study area paralleled the ecotone between Crowley's Ridge, a loess formation of Pleistocene age, and the floodplain of the St. Francis and Mississippi rivers. Second growth forest along the census transect included typical floodplain taxa (e.g., *Carya aquatica*) as well as those species restricted within the Mississippi Embayment to Crowley's Ridge (e.g., *Lireodendron tulipifera*). Soils were Convent silt loams (coarse-silty, mixed, nonacid, thermic Aeric Fluvaquents; Hogan and Gray 1974, Gray 1977). Males establish breeding territories on the Gulf Coastal plain and in the lower Mississippi Valley during the second and third weeks of April (Meanley 1971, Brown and Dickson 1994). I marked foraging sites 4–7 May 1993 ($n = 6$) and collected habitat data 5–7 May 1993. Population density in the study area was ca 3.8 males/km².

(2) Sunflower River (32° 51' N, 90° 46' W), Delta National Forest, Sharkey County, Mississippi. I sampled territories on the floodplain of the Big Sunflower River in second growth forest ($n = 7$) and in the largest remaining tract of old growth forest ($n = 3$) in the Mississippi Delta, all on Sharkey clay soils (very-fine, montmorillonitic, nonacid, thermic Vertic Haplaquepts; Scott and Carter 1962). I marked foraging sites from 25 April to 1 May 1993 and collected habitat data from 28 April to 2 May 1993. Population density in the study area was ca 4.8–9.3 males/km².

(3) Whiskey Bay Pilot Channel (30° 24' N, 91° 40' W), Sherburne Wildlife Management Area and Atchafalaya National Wildlife Refuge, St. Martin Parish, Louisiana. The study site on the east bank of the main channel of the Atchafalaya River was dominated by second growth deciduous forest (10–50 years old) on Convent silt loam soils (Murphy et al. 1977). The eye of Hurricane Andrew passed directly over the study area on 26 August 1992, causing moderate canopy

damage and scattered windthrow (Doyle et al. 1995). I marked foraging and nesting sites from 26 April to 10 May 1994 ($n = 14$ foraging sites; $n = 3$ nests) and 10 May 1995 ($n = 1$ nest); B. L. Tedford collected habitat data from 27 April to 30 June 1994 and on 10 June 1995. Population density in the study area was ca 11.3–14.2 males/km².

(4) Pearl River (30° 25' N, 89° 43' W), Bogue Chitto National Wildlife Refuge and Pearl River Wildlife Management Area, St. Tammany Parish, Louisiana. The study site on the floodplain of the Pearl River was characterized by second growth forest of mixed age (10–60 years old) on Arkatbutla and Rosebloom soils (fine-silty, mixed, acid, thermic Aeric Fluvaquents; Trahan et al. 1990). I marked foraging sites from 25 April to 6 May 1995 ($n = 7$ territories); B. L. Tedford collected habitat data 1–23 July 1995. Population density in the study area was ca 20.5 males/km².

(5) Apalachicola River (30° 04' N, 89° 43' W), Liberty County, Florida. The study site on the floodplain of the Apalachicola River in the Apalachicola National Forest was a patchwork of regenerating clearcuts (mostly 1–8 m high) and tracts of taller second growth deciduous and mixed deciduous-pine forest (20–30 m) on Meggett loam soils (fine, mixed, thermic Typic Albauqualls; USDA Soil Conservation Service unpubl. data). I marked foraging sites 28–30 April 1996 ($n = 12$ territories); B. L. Tedford collected habitat data 9–13 June 1996. Population density in the study area was ca 5.6 males/km².

Statistics and hypothesis testing.—I tested variables for goodness of fit to a normal distribution with Lilliefors test. Nine of 14 variables exhibited significant deviations from normality even after being subjected to variance-stabilizing transformations. Therefore, I used a series of nonparametric one-way analysis of variance tests (Kruskal-Wallis ANOVA) to evaluate geographic variation among physiognomic and floristic variables (Table 1). Significance values were Bonferroni adjusted for the number of simultaneous tests ($P = 0.05/14$). The univariate relationship between selected pairs of variables was evaluated with Spearman rank correlation coefficients. Covariation among variables was evaluated with principal components analysis (PCA) of correlation matrices for transformed variables. This procedure transforms a group of generally correlated variables into a set of uncorrelated composite variables and is particularly useful for reducing the dimensionality of complex data sets for graphic presentation. All analyses were performed with SYSTAT ver. 9 (SPSS, Inc. 1998).

RESULTS

Kruskal-Wallis ANOVA revealed significant geographic variation in 8 of the 14 habitat variables, although locality medians were relatively similar in magnitude for most variables (Table 1). For example, although the basal area of trees (BAS) on individual plots had a range of 6.1–87.4 m²/ha, locality me-

TABLE 1. Ranges (medians) of physiognomic and floristic variables measured on 0.045-ha plots in 53 territories of the Swainson's Warbler at five localities in the core breeding range of the species in the southeastern United States, 1993–1996.

Code	Variable	Localities					Kruskal-Wallis ANOVA	
		Crowley's Ridge (n = 6)	Sunflower River (n = 10)	Whiskey Bay (n = 18)	Pearl River (n = 7)	Appalachicola River (n = 12)	χ^2	P ^a
BAS	Total basal area of trees (dbh > 5 cm) m ² /ha	21.7–52.8 (26.0)	14.6–87.4 (29.3)	9.3–33.1 (16.8)	7.8–16.0 (13.0)	6.1–42.9 (13.7)	19.60 (18.2) ^b	0.0006
ONE	Trees (dbh = 5–14.9 cm)/ha	333–1,244 (467)	111–422 (233)	422–1,956 (711)	378–644 (489)	178–1,111 (644)	21.32 (511)	0.0003
TWO	Trees (dbh = 15–24.9 cm)/ha	44–133 (122)	22–222 (67)	22–356 (111)	111–378 (133)	44–289 (100)	6.69 (111)	0.15
THRE	Trees (dbh = 25–39.9 cm)/ha	0–133 (67)	0–133 (56)	0–133 (89)	0–89 (44)	0–244 (44)	4.62 (44)	0.33
FOUR	Trees (dbh = 40–59.9 cm)/ha	0–89 (33)	0–67 (33)	0–89 (0)	0–44 (0)	0–156 (11)	7.85 (22)	0.097
FIVE	Trees (dbh = 60–79.9 cm)/ha	0–89 (22)	0–22 (0)	0–22 (0)	0 (0)	0–22 (0)	22.96 (0)	0.0001
SIX	Trees (dbh > 80 cm)/ha	0 (0)	0–44 (0)	0–22 (0)	0 (0)	0 (0)	13.86 (0)	0.008
TREE	Trees (dbh > 5 cm)/ha	600–1,422 (789)	267–822 (433)	667–2,156 (1,044)	555–1,022 (689)	289–1,267 (878)	20.50 (778)	0.0004
TSPE	Tree species (dbh > 5 cm)/0.045 ha	7–15 (11.5)	4–10 (5.5)	5–13 (8)	6–10 (8)	3–9 (7)	16.93 (8)	0.002
VINE	Vines (including <i>Smilax</i>) supported by trees/ha	2,773–15,067 (5,111)	2,044–7,089 (4,578)	755–5,955 (2,444)	1,600–5,755 (3,111)	222–3,267 (1,022)	25.87 (2,744)	<0.0001
VSPE	Vine species/0.045 ha	8–11 (9.5)	7–9 (9)	3–9 (6)	8–12 (9)	2–8 (5)	34.92 (8)	<0.0001
CANE	Cane culms/ha	0–1,987 (0)	0–73,118 (0)	0 (0)	0 (0)	0 (0)	10.64 (0)	0.03
SHRU	Woody stems (dbh < 5 cm)/ha	17,087–79,476 (44,903)	8,742–63,183 (28,313)	7,550–104,710 (34,969)	32,983–58,018 (48,281)	20,465–59,607 (32,585)	5.45 (34,773)	0.24
SSPE	Shrub species/50.3 m ² (including tree saplings)	13–29 (17.5)	8–19 (15.5)	7–22 (14)	17–22 (20)	14–23 (17)	17.22 (16)	0.002

^a Bonferroni adjustment: 0.05/14 = 0.0036; 0.01/14 = 0.0004; 0.001/14 = 0.00007.

^b Median of data pooled across study sites.

TABLE 2. Tree species that composed more than 5% of the stems (dbh > 5 cm) in 53 territories of the Swainson's Warbler at five localities in the core breeding range of the species in the southeastern United States, 1993–1996. Total number of tree species at each locality is given in parentheses; values are percentages.

Tree species	Locality				
	Crowley's Ridge (28)	Sunflower River (17)	Whiskey Bay (23)	Pearl River (22)	Apalachicola River (18)
<i>Liquidambar styraciflua</i> (sweet gum)	12.2	14.8	—	25.1	18.1
<i>Ulmus americana</i> (American elm)	13.5	13.9	6.4	—	—
<i>Acer rubrum</i> (red maple)	—	7.2	7.4	—	5.2
<i>Quercus nigra</i> (water oak)	—	—	—	22.4	12.0
<i>Acer negundo</i> (box elder)	—	11.5	20.6	—	—
<i>Celtis laevigata</i> (sugarberry)	—	28.7	—	—	—
<i>Cornus drummondii</i> (rough-leaved dogwood)	—	—	26.0	—	—
<i>Carpinus caroliniana</i> (American hornbeam)	—	—	—	23.3	—
<i>Pinus elliotii</i> (slash pine)	—	—	—	—	20.0
<i>Liriodendron tulipifera</i> (tulip poplar)	13.5	—	—	—	—
<i>Myrica cerifera</i> (wax myrtle)	—	—	—	—	11.1
<i>Forestiera acuminata</i> (swamp privet)	—	8.6	—	—	—
<i>Fraxinus pennsylvanica</i> (green ash)	—	—	8.1	—	—
<i>Sassafras albidum</i> (sassafras)	7.0	—	—	—	—
<i>Platanus occidentalis</i> (sycamore)	—	—	7.0	—	—
<i>Cyrilla racemiflora</i> (titi)	—	—	—	—	6.8
<i>Halesia diptera</i> (two-winged silverbell)	—	—	—	6.7	—
<i>Quercus laurifolia</i> (laurel oak)	—	—	—	—	6.6
<i>Nyssa sylvatica</i> (black gum)	—	—	—	—	6.6

dians varied from 13.0 m²/ha (Pearl River) to 29.3 m²/ha (Sunflower River). Substantial variability in basal area indicated that canopy height was a relatively unimportant factor influencing habitat use. Vegetation plots at all study sites were dominated by trees in the smallest size class (dbh = 5.0–14.9 cm; ONE), with locality medians varying from 233 trees/ha (Sunflower River) to 711 trees/ha (Whiskey Bay). The number of small trees (ONE) was highly correlated with the total number of trees (TREE) on vegetation plots ($r_s = 0.96$, $P < 0.0001$). There was no significant difference among sites in the frequencies of medium-sized trees (TWO, THREE, FOUR).

Scattered understory thickets composed of tree saplings, shrubs, and vines were the most conspicuous characteristic of breeding territories across the five study sites. The density of small woody stems (SHRU) on vegetation plots varied from 7,550–104,710 stems/ha. Locality medians for understory stems (SHRU + CANE) fell within a relatively narrow range of possible values: Sunflower River (31,592 stems/ha); Apalachicola River (32,585 stems/ha); Whiskey Bay (34,969 stems/ha); Crowley's Ridge (44,903 stems/

ha); and Pearl River (48,281 stems/ha). The number of small trees (ONE) and small woody stems (SHRU) was uncorrelated ($r_s = -0.03$, $P = 0.83$).

High vine densities frequently were associated with canopy gaps and successional habitats favored by Swainson's Warblers. Regional variation in median vine density ranged from 1,022 vines/ha (Apalachicola River) to 5,111 vines/ha (Crowley's Ridge). The number of vines (VINE) and small woody stems in the understory (SHRU) was not significantly correlated ($r_s = 0.23$, $P = 0.091$). Giant cane (CANE) was uncommon at Crowley's Ridge (1 of 6 plots) and the Sunflower River (2 of 10 plots), and not observed at Whiskey Bay. Although scattered patches of cane occurred on the floodplains of the Pearl and Apalachicola rivers, none was recorded in vegetation plots in those areas.

The number of tree species (TSPE) per site ranged from 17 (Sunflower River) to 28 (Crowley's Ridge; Table 2). The high floristic diversity at Crowley's Ridge reflected a mixture of taxa restricted in eastern Arkansas to loess hills (e.g., *Liriodendron tulipifera*) with those species typical of floodplain habitats (e.g., *Carya aquatica*, *Liquidambar styraci-*

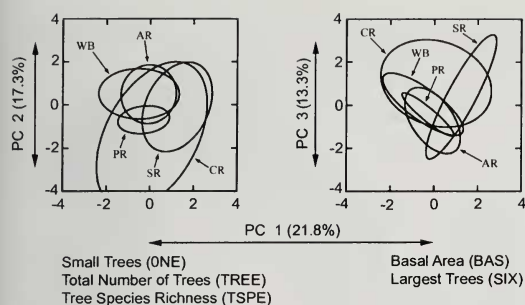


FIG. 2. Bivariate plots of 80% confidence ellipses surrounding factor scores produced by a principal components analysis of physiognomic and floristic variables of Swainson's Warbler habitat. Arrow indicates the direction of component loadings for variables that strongly influence the first principal component (PC 1). Locality codes: Apalachicola River (AR), Crowley's Ridge (CR), Pearl River (PR), Sunflower River (SR), and Whiskey Bay (WB).

flua). Cumulative species richness at each site was uncorrelated with the number of territories sampled ($r_s = -0.34$, $P = 0.34$). However, species richness within plots was positively correlated with the number of trees sampled ($r_s = 0.34$, $P = 0.013$). Each locality was dominated by a different species of tree, but no species composed more than 5% of the stems (>5 cm dbh) at each of the five study sites. The forest canopy at all localities was composed primarily of broad-leaved trees, although slash pine (*Pinus elliotii*) was frequent at the Apalachicola River site. The scarcity of hydrophytic species, such as bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*), indicated that foraging and nesting sites were not subjected to prolonged flooding during the growing season (Table 2). Intra- and interlocality variation in the flora of territories offered additional confirmation that the warbler's breeding biology in floodplain habitats was not tied to the presence of a particular plant species (Graves 2001).

A principal components analysis of 14 habitat variables yielded three components (eigenvalues >1.5), which accounted for about half (52.4%) the variation recorded on plots in Swainson's Warbler territories (Fig. 2, Table 3). Principal component 1 (21.8% of the variance) discriminated vegetation plots with large trees (SIX) and high basal areas (BAS) from floristically rich plots (TSPE) with many small trees (ONE, TREE). Principal compo-

TABLE 3. Principal component analysis of the correlation matrix among 14 physiognomic and floristic variables in 53 plots in territories of Swainson's Warbler in its core breeding range in the lower Mississippi Valley and along the Gulf coastal plain, 1993–1996. Correlation loadings >0.50 or <-0.50 are in boldface. Variable codes are presented in Table 1.

Variables	PC 1	PC 2	PC 3
BAS	0.68	0.03	0.59
ONE	-0.81	0.23	0.36
TWO	-0.44	0.17	0.23
THRE	0.36	0.40	-0.18
FOUR	0.38	0.12	0.03
FIVE	0.30	-0.42	0.33
SIX	0.58	0.04	0.51
TREE	-0.78	0.31	0.41
TSPE	-0.52	-0.42	0.49
VINE	-0.03	-0.72	0.33
VSPE	0.20	-0.53	0.28
CANE	0.30	0.31	0.31
SHRU	-0.13	-0.56	-0.38
SSPE	-0.14	-0.71	-0.29

nent 2 (17.3% of the variance) represented a vine and shrub element separating plots with high and low counts of species (VSPE, SSPE) and stems (VINE, SHRU). Principal component 3 (13.3% of the variance) exhibited positive loadings for large trees (SIX) and basal area (BAS), variables which also figured prominently on the first component. Although factor scores differed significantly among localities (Kruskal-Wallis ANOVA of locality medians; PC 1: $\chi^2 = 19.90$, $df = 4$, $P = 0.001$; PC 2: $\chi^2 = 26.19$, $df = 4$, $P < 0.001$; PC 3: $\chi^2 = 14.32$, $df = 4$, $P = 0.006$), the overlap of concentration ellipses surrounding factor scores indicated that intralocality variability accounted for much of the observed variation.

DISCUSSION

Understory stem density in early successional floodplain forest in the southeastern United States frequently exceeds 200,000 stems/ha (GRG unpubl. data). However, the maximum count of stems (SHRU + CANE) observed on Swainson's Warbler territories in the core breeding range (104,710 stems/ha) and in the Great Dismal Swamp, southeastern Virginia (81,400 stems/ha; Graves 2001), was about half that value. These data indicate that habitat quality is not linearly correlated with the abundance of small woody stems. Instead,

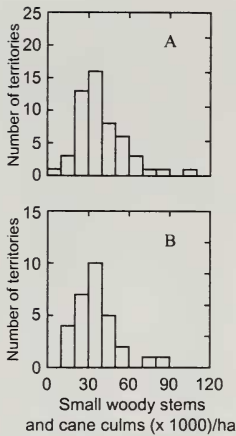


FIG. 3. Density of small woody stems and cane culms in territories of the Swainson's Warbler: (A) pooled data from five study sites in the core breeding range reported in this paper, and (B) data from the Great Dismal Swamp, southeastern Virginia (Graves 2001).

a relatively narrow range of stem densities (ca 30,000–50,000 stems/ha) appears to provide high quality cover for nesting and foraging throughout its breeding range (Table 1). Counts of understory stems (SHRU + CANE) pooled across the five study sites in the core breeding range ($n = 53$ territories, median = 34,773 stems/ha; Table 1) were not statistically different (Kruskal-Wallis ANOVA, $\chi^2 = 0.73$, $df = 1$, $P = 0.39$) from comparable data collected with identical sampling techniques in the Great Dismal Swamp ($n = 30$ territories; median = 36,220 stems/ha; Fig. 3). Investigations at other locations reported a wider range of mean stem densities on breeding territories: southern Illinois (small woody stems and cane: mean = 26,390 stems/ha; Eddleman et al. 1980); southern Missouri (cane: mean = 61,000 culms/ha; Thomas et al. 1996); central Georgia (cane: mean = ca 50,000 culms/ha; Meanley 1966); and South Carolina (small woody stems: mean = 99,836 stems/ha; Hamel 1981). I suspect that a significant fraction of this variation may be attributed to marked differences in vegetation sampling techniques. The apparent absence of giant cane in the Whiskey Bay corridor, perhaps the premier Swainson's Warbler locality in terms of total breeding population, should put to rest the hypothesis first proposed by

Brewster (1885) that cane is an essential component of prime habitat.

Contemporary management strategies for the Swainson's Warbler call for the preservation of large blocks of unfragmented forest (Eddleman et al. 1980, Hunter et al. 1994, Mueller et al. 2000), the maintenance and regeneration of canebrakes (Eddleman et al. 1980, Thomas et al. 1996), the creation of small canopy gaps by selective cutting (Eddleman et al. 1980, Pashley and Barrow 1993), and the generation of larger (≤ 1.6 ha) gaps through clearcutting (Eddleman et al. 1980). On the other hand, Dickson et al. (1993) suggested that populations would benefit by setting aside mature floodplain forests and allowing young stands of trees to mature. As previously suggested (Graves 2001), data from the core breeding range support the hypothesis that Swainson's Warblers prefer early successional forest in the current landscape or disturbance gaps in old growth forest.

In the remainder of this paper I discuss some aspects of habitat management for the Swainson's Warbler. First, the hydroperiod of reserves managed for this species must be compatible with the warbler's terrestrial foraging behavior (Graves 2001). Breeding territories are restricted to moist soils, but flooding is a potent determinant of habitat occupancy patterns on local and regional scales (Meanley 1966, 1971; Graves 2001). Ideally, water levels should be maintained at or below ground level from late March through September. Furthermore, annual winter and spring flooding should not be so intense as to scour and wash away the accumulated bank of leaf litter and detritus, which constitutes the critical foraging substrate on the breeding and wintering grounds (Meanley 1970; Graves 1996, 1998, 2001; Strong 2000). It is unfortunate that a substantial fraction of the remaining tracts of floodplain forest on the coastal plain and in the lower Mississippi Valley (see map in Twedt and Loesch 1999) is subject to annual flooding during the breeding season. In essence, the calculation of effective area of Swainson's Warbler reserves should begin with the subtraction of chronically flooded zones.

Although the area requirements for viable breeding populations of Swainson's Warblers are believed to be substantial owing to its



FIG. 4. Physiognomic profile of habitat elements typically associated with breeding territories of the Swainson's Warbler in its core breeding range: (A) vine "tents" and tangles; (B) small shaded glades carpeted with leaf litter; and (C) thickets of shrubs, tree saplings, vines, and *Rubus* spp. associated with canopy gaps. Giant cane (D) is rare or absent from many prime breeding sites in the lower Mississippi Valley.

large territory size and relatively low population density (Eddleman et al. 1980, Brown and Dickson 1994, Hunter et al. 1994), the degree to which it tolerates forest fragmentation is unknown. Estimated population densities reported in this paper ranged from 3.8–20.5 males/km². The latter figure represented the highest density estimate obtained with standardized censuses along linear transects >3.5 km in length (GRG unpubl. data). Densities of 5–8 pairs/km² are perhaps attainable in multipurpose floodplain reserves. Using this range of density values as a guideline, reserves capable of supporting 500 pairs of Swainson's Warblers would vary in size from 6,250–10,000 ha, or approximately 2.78–4.44 times larger than the minimum area requirement suggested by Hunter et al. (1994).

The dense breeding populations (10–20 territorial males/km²) of Swainson's Warblers encountered at Whiskey Bay and Pearl River occurred in successional floodplain forest dominated by small (<25 cm dbh) trees (ca 620–820 stems/ha) and understory thickets (ca 35,000–48,000 small woody stems/ha). In these localities and many others across the warbler's breeding range (Eddleman et al. 1980, Brown and Dickson 1994, Thomas et al. 1996, Graves 2001), canopy height, basal area, and floristics appear to be relatively unimportant factors in habitat selection, provid-

ed that understory requisites are met—which explains the warbler's occurrence in regenerating clearcuts as well as in old growth forest. Breeding density is far lower (typically <2.0 males/km²) in taller, more mature forests characterized by a closed canopy and relatively sparse undergrowth (<10,000 small woody stems/ha; GRG unpubl. data). Territories in such habitat typically are centered at large disturbance gaps dominated by luxuriant thickets of tree saplings, shrubs, and woody vines (Fig. 4).

The attractiveness of closed canopy forests to Swainson's Warblers can be enhanced by selective thinning or the creation of small clearcuts (Eddleman et al. 1980, Pashley and Barrow 1993). Selective thinning, to the extent needed to simulate optimal habitat, may be logistically unfeasible and too labor intensive to be uniformly applied to large (ca 5,000–10,000 ha) reserves of maturing secondary forest. The generation of small clearcuts, spatially configured to serve as territorial nuclei, may be a more practical management alternative. The optimal size of clearcuts will depend upon the overall quality of the habitat. Experimental evidence from the Great Dismal Swamp suggests that clearcuts as small as 0.25 ha (at a density of 25 clearcuts/km²) may induce Swainson's Warblers to colonize marginal habitat (GRG unpubl. data). Larger (0.5–

1.0 ha) clearcuts may be more effective attractors, but a variety of cutting and thinning protocols is likely to yield satisfactory outcomes.

Habitat management on agroforestry lands in the southeastern United States requires a different strategy, however, especially with the proliferation of high capacity wood chip mills, which encourage large scale clearcutting of young deciduous forests (trees as small as 7.5 cm dbh) for pulp. The possibility that the Swainson's Warbler may not perceive agroforestry landscapes as excessively fragmented is suggested by the documented occurrence of breeding in regenerating clearcuts (Eddleman et al. 1980, Brown and Dickson 1994, Peters 1999), young pine plantations (Carrie 1996, Bassett 2001, GRG unpubl. data) and large disturbance gaps in mature forests (GRG unpubl. data). In fact, mosaics of regenerating clearcuts (6–30 years old) frequently support robust breeding populations (Peters 1999; GRG unpubl. data). To facilitate colonization and occupancy of agroforestry lands on floodplains, pulpwood producers should be encouraged to make relatively small (10–20 ha) clearcuts on a staggered 25-year cutting rotation.

ACKNOWLEDGMENTS

I owe special thanks to B. L. Tedford for collecting vegetation data under some of most physically demanding conditions in the southeastern United States. I am grateful to W. C. Barrow, R. E. Brown, and J. A. Gerwin for critiquing the manuscript. Gerwin also provided a photocopy of K. A. Peters' thesis. I thank the staffs of the Apalachicola National Forest, Bogue Chitto National Wildlife Refuge, Delta National Forest, and St. Francis National Forest for information and assistance. The project was funded by the Smithsonian Research Opportunities Fund and the U.S. Fish and Wildlife Service (14-48-0005-92-9013 and 14-48-0009-946).

LITERATURE CITED

- BASSETT, C. A. 2001. Habitat selection of the Swainson's Warbler in managed forests in southeastern Louisiana. M.Sc. thesis, Southeastern Louisiana Univ., Hammond.
- BECKHAM, C. W. 1887. Additions to the avi-fauna of Bayou Sara, La. *Auk* 4:299–306.
- BREWSTER, W. 1885. Swainson's Warbler. *Auk* 2:65–80.
- BROOKS, M. AND W. C. LEGG. 1942. Swainson's Warbler in Nicholas County, West Virginia. *Auk* 59:76–86.
- BROWN, R. E. AND J. G. DICKSON. 1994. Swainson's Warbler (*Limnothlypis swainsonii*). No. 126 in *The birds of North America* (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, Pennsylvania, and the American Ornithologists' Union, Washington, D.C.
- CARRIE, N. R. 1996. Swainson's Warblers nesting in early seral pine forests in East Texas. *Wilson Bull.* 108:802–804.
- COLLINS, S. L. 1983a. Geographic variation in habitat structure of the Black-throated Green Warbler (*Dendroica virens*). *Auk* 100:382–389.
- COLLINS, S. L. 1983b. Geographic variation in habitat structure for the wood warblers in Maine and Minnesota. *Oecologia* 59:246–252.
- DICKSON, J. G., F. R. THOMPSON, III, R. N. CONNOR, AND K. E. FRANZREB. 1993. Effects of silviculture on Neotropical migratory birds in central and southern oak-pine forests. Pp. 374–385 in *Status and management of Neotropical migratory birds* (D. M. Finch and P. W. Stangel, Eds.). U.S. Forest Service Gen. Tech. Rept. RM-229, Fort Collins, Colorado.
- DOW, D. D. 1968. Home range and habitat of the Cardinal in peripheral and central populations. *Can. J. Zool.* 47:103–114.
- DOYLE, T. W., B. D. KEELAND, L. E. GORHAM, AND D. J. JOHNSON. 1995. Structural impact of Hurricane Andrew on the forested wetlands of the Atchafalaya Basin in south Louisiana. *J. Coastal Res.* 21:354–364.
- EDDLEMAN, W. R. 1978. Selection and management of Swainson's Warbler habitat. M.Sc. thesis, Univ. of Missouri, Columbia.
- EDDLEMAN, W. R., K. E. EVANS, AND W. H. ELDER. 1980. Habitat characteristics and management of Swainson's Warbler in southern Illinois. *Wildl. Soc. Bull.* 8:228–233.
- GRAVES, G. R. 1992. A case of aggregated nest placement and probable polygyny in the Swainson's Warbler. *Wilson Bull.* 104:370–373.
- GRAVES, G. R. 1996. Censusing wintering populations of Swainson's Warblers: surveys in the Blue Mountains of Jamaica. *Wilson Bull.* 108:94–103.
- GRAVES, G. R. 1998. Stereotyped foraging behavior of the Swainson's Warbler. *J. Field Ornithol.* 69:121–127.
- GRAVES, G. R. 2001. Factors governing the distribution of Swainson's Warbler along a hydrological gradient in Great Dismal Swamp. *Auk* 118:650–664.
- GRAVES, G. R., M. B. SIMPSON, JR., AND L. D. STEPHENS. 1996. Joseph LeConte and the discovery of the nest of Swainson's Warbler (*Limnothlypis swainsonii*): a reconsideration. *Arch. Nat. Hist.* 23:287–290.
- GRAY, J. L. 1977. Soil survey of Lee County, Arkansas. USDA Soil Conservation Service and Forest Service, Washington, D.C.
- HAMEL, P. B. 1981. A hierarchical approach to avian community structure. Ph.D. diss., Clemson Univ., Clemson, South Carolina.

- HOGAN, J. L. AND J. L. GRAY. 1974. Soil survey of Phillips County, Arkansas. USDA Soil Conservation Service and Forest Service, Washington, D.C.
- HUNTER, W. C., A. J. MUELLER, AND C. L. HARDY. 1994. Managing for Red-cockaded Woodpeckers and Neotropical migrants—is there a conflict? Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 48:383–394.
- HUNTER, W. C., D. N. PASHLEY, AND R. E. F. ESCANO. 1993. Neotropical migratory landbird species and their habitats of special concern within the southeast region. Pp. 159–171 in Status and management of Neotropical migratory birds (D. M. Finch and P. W. Stangel, Eds.). U.S. Forest Service General Technical Report RM-229, Fort Collins, Colorado.
- JAMES, F. C., C. A. HESS, AND D. KUFRIN. 1997. Species-centered environmental analysis: indirect effects of fire history on the Red-cockaded Woodpecker. Ecol. Appl. 7:118–129.
- JAMES, F. C., R. F. JOHNSTON, N. G. WAMER, G. J. NIEMI, AND W. J. BOECKLEN. 1984. The Grinnellian niche of the Wood Thrush. Am. Nat. 124:17–30.
- KUCHLER, A. W. 1966. Potential natural vegetation. U.S. Geological Survey Sheet No. 90, Washington, D.C.
- MEANLEY, B. 1945. Notes on Swainson's Warbler in central Georgia. Auk 62:395–401.
- MEANLEY, B. 1966. Some observations on habitats of the Swainson's Warbler. Living Bird 5:151–165.
- MEANLEY, B. 1969. Pre-nesting and nesting behavior of the Swainson's Warbler. Wilson Bull. 81:246–257.
- MEANLEY, B. 1970. Method of searching for food by the Swainson's Warbler. Wilson Bull. 82:228.
- MEANLEY, B. 1971. Natural history of the Swainson's Warbler. N. Am. Fauna 69:1–90.
- MORSE, D. H. 1989. American warblers: an ecological and behavioral perspective. Harvard Univ. Press, Cambridge, Massachusetts.
- MUELLER, A. J., D. J. TWEDT, AND C. R. LOESCH. 2000. Development of management objectives for breeding birds in the Mississippi Alluvial Valley. Pp. 12–17 in Strategies for bird conservation: the Partners in Flight planning process (R. Bonney, D. N. Pashley, R. J. Cooper, and L. Niles, Eds.). Proceedings of the 3rd Partners in Flight Workshop, October 1–5, 1995, Cape May, New Jersey. Proceedings RMRS-P-16. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah.
- MURPHY, K. E., B. A. TOUCHET, A. G. WHITE, J. J. DAIGLE, AND H. L. CLARK. 1977. Soil survey of St. Martin Parish, Louisiana. USDA Soil Conservation Service, Washington, D.C.
- ORIAN, G. H. AND J. F. WITTENBERGER. 1991. Spatial and temporal scales in habitat selection. Am. Nat. 137:S29–S49.
- PARRISH, J. D. 1995. Effects of needle architecture on warbler habitat selection in a coastal spruce forest. Ecology 76:1813–1820.
- PASHLEY, D. N. AND W. C. BARROW. 1993. Effects of land use practices on Neotropical migratory birds in bottomland hardwood forests. Pp. 315–320 in Status and management of Neotropical migratory birds (D. M. Finch and P. W. Stangel, Eds.). U.S. Forest Service General Technical Report RM-229, Fort Collins, Colorado.
- PETERS, K. A. 1999. Swainson's Warbler (*Limnothlypis swainsonii*) habitat selection in a managed bottomland hardwood forest in South Carolina. M.Sc. thesis, North Carolina State Univ., Raleigh.
- POOLE, A. AND F. GILL (EDS.). 1993–1997. The birds of North America, Nos. 41–320. Academy of Natural Sciences, Philadelphia, Pennsylvania, and the American Ornithologists' Union, Washington, D.C.
- POOLE, A. AND F. GILL (EDS.). 1998–2002. The birds of North America, Nos. 321–640. Birds of North America, Inc., Philadelphia, Pennsylvania.
- POOLE, A., P. STETTENHEIM, AND F. GILL (EDS.). 1992–1993. The birds of North America, Nos. 1–40. Academy of Natural Sciences, Philadelphia, Pennsylvania, and the American Ornithologists' Union, Washington, D.C.
- RAPPOLE, J. H. 1995. The ecology of migrant birds. Smithsonian Inst. Press, Washington, D.C.
- REMSEN, J. V., JR. 2001. The true winter range of the Veery (*Catharus fuscescens*): lessons for determining winter ranges of species that winter in the tropics. Auk 118:838–848.
- ROBBINS, C. S., J. W. FITZPATRICK, AND P. B. HAMEL. 1992. A warbler in trouble: *Dendroica cerulea*. Pp. 549–562 in Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan, III and D. W. Johnston, Eds.). Smithsonian Inst. Press, Washington, D.C.
- ROBINSON, S. K. AND R. T. HOLMES. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. Auk 101:672–684.
- SCOTT, F. T. AND R. C. CARTER. 1962. Soil survey of Sharkey County, Mississippi. USDA Soil Conservation Service, Washington, D.C.
- SIMS, E. AND W. R. DEGARMO. 1948. A study of Swainson's Warbler in West Virginia. Redstart 16: 1–8.
- SMITH, C. R., D. M. PENCE, AND R. J. O'CONNOR. 1993. Status of Neotropical migratory birds in the northeast: a preliminary assessment. Pp. 172–188 in Status and management of Neotropical migratory birds (D. M. Finch and P. W. Stangel, Eds.). U.S. Forest Service General Technical Report RM-229, Fort Collins, Colorado.
- SPSS, INC. 1998. SYSTAT, ver. 9. SPSS, Inc., Chicago, Illinois.
- STOWE, T. J., A. V. NEWTON, R. E. GREEN, AND E. MAYES. 1993. The decline of the Corncrake *Crex crex* in Britain and Ireland in relation to habitat. J. Appl. Ecol. 30:53–62.
- STRONG, A. M. 2000. Divergent foraging strategies of two Neotropical migrant warblers: implications for winter habitat use. Auk 117:381–392.

- TERBORGH, J. 1989. Where have all the birds gone? Princeton Univ. Press, Princeton, New Jersey.
- THOMAS, B. G., E. P. WIGGERS, AND R. L. CLAWSON. 1996. Habitat selection and breeding status of Swainson's Warbler in southern Missouri. *J. Wildl. Manage.* 60:611-616.
- THOMPSON, F. R., S. J. LEWIS, J. GREEN, AND D. EWERT. 1993. Status of Neotropical migrant landbirds in the Midwest: identifying species of management concern. Pp. 145-158 *in* Status and management of Neotropical migratory birds (D. M. Finch and P. W. Stangel, Eds.). U.S. Forest Service General Technical Report RM-229, Fort Collins, Colorado.
- TRAHAN, L., J. J. BRADLEY, AND L. MORRIS. 1990. Soil survey of St. Tammany Parish, Louisiana. USDA Soil Conservation Service, Washington, D.C.
- TWEDT, D. J. AND C. R. LOESCH. 1999. Forest area and distribution in the Mississippi alluvial valley: implications for breeding bird conservation. *J. Biogeogr.* 26:1215-1224.
- WAYNE, A. T. 1886. Nesting of Swainson's Warbler in South Carolina. *Ornithologist and Oologist* 11: 187-188.
- WIDMANN, O. 1895. Swainson's Warbler: an inhabitant of the swampy woods of southeastern Missouri. *Auk* 12:112-117.
- WIENS, J. A. 1989. The ecology of bird communities. Cambridge Univ. Press, Cambridge, Massachusetts.
- WINKER, K., G. R. GRAVES, AND M. J. BRAUN. 2000. Genetic differentiation among populations of a migratory songbird: *Limnithlypis swainsonii*. *J. Avian Biol.* 31:319-328.